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Research article

Maladaptive nest-site selection by a sagebrush dependent species in a grazing-modified landscape

Kyle A. Cutting[a,b,c,*], Jay J. Rotella[b], Sean R. Schroff[c], Michael R. Frisina[c], James A. Waxe[a,b], Erika Nunlist[c], Bok F. Sowell[c]

[a] Red Rock Lakes National Wildlife Refuge, U.S. Fish and Wildlife Service, 27650B South Valley Road, Lakeview, MT 59739, USA
[b] Department of Ecology, Montana State University, 310 Lewis Hall, Bozeman, MT 59717, USA
[c] Department of Animal and Range Sciences, Montana State University, Animal Bioscience Building 205, Bozeman, MT 59717, USA

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ABSTRACT

Animals are expected to select habitats that maximize their fitness over evolutionary time scales. Yet in human-modified landscapes, habitat selection might not always lead to increased fitness because animals undervalue high-quality resources that appear less attractive than those of lower quality. In the American West, agriculture has modified landscapes, yet little is known about whether agricultural changes alter the reliability of the cues animals use to identify habitat quality; ultimately forming maladaptive breeding strategies where behavioral cues are mismatched with survival outcomes.

Using the greater sage-grouse, a species highly dependent upon sagebrush landscapes, we (1) evaluated how females select nesting habitats based on sagebrush type, along with livestock grazing related linear and point features, and other biotic, abiotic characteristics, given hypothesized influences on hiding cover, microclimate and predator travel routes and perches, (2) compared habitat selection information with results for nest survival estimates to evaluate if selection appears to be adaptive or not, and (3) used our results to evaluate the most appropriate strategies for this species in a grazing-modified landscape. Nest-site selection for sagebrush type appears to be maladaptive: in the most-preferred sagebrush type, nest survival rate was one-fourth the rate realized by females nesting in the sagebrush type avoided. Nest survival was four times higher for nests placed away from (> 100 m), rather than next to (1 m), the nearest fence, and survival was lower within sites with higher cow pie density (a proxy for previous grazing intensity). Live and dead grasses influenced selection and survival in opposing ways such that dead grass was selected for but resulted in reduced survival while live grass was avoided but resulted in increased survival. Results collectively provide the first empirical evidence that a specific type of sagebrush acts as an ecological trap while another sagebrush type is undervalued. These results also suggest that adding more fences to control livestock grazing systems will likely reduce sage-grouse nest survival.

1. Introduction

Habitat selection evolved under natural selection, and its influence on subsequent fitness in avian taxa has been widely demonstrated (Clark and Shutler, 1999). Many animals rely on environmental cues to assess a site's potential to maximize their fitness (Southwood, 1977). These cues include tracking changes in food abundance, predators, and diverse environmental features. In dynamic landscapes, an animal's ability to track changes in resources can sometimes be inadequate to adapt to rapid environmental change (Hollander et al., 2017). In human-modified landscapes, numerous examples have been documented where animals select low-quality habitats even when high-quality ones exist in a scenario defined as an ecological trap (Robertson et al., 2013). Similarly, mechanisms that create ecological traps have corollaries that create undervalued resources; which in theory occur when high-quality resources appear less attractive than lower quality ones (Robertson and Chalfoun, 2016). Yet, few empirical data exist that show how both forms of maladaptation govern adaptive selection across different habitat types (Robertson and Chalfoun, 2016).

The sagebrush (*Artemisia* spp.) biome of the American West is one of the largest ecotypes in North America, yet it constitutes one of the twenty-two most imperiled major ecosystems in the United States (Noss et al., 1995). The biome has been reduced to half of its historical extent due to fragmentation and conversion for livestock forage, energy

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* Corresponding author. Red Rock Lakes National Wildlife Refuge, U.S. Fish and Wildlife Service, 27650B South Valley Road, Lakeview, MT 59739, USA.
E-mail address: Kyle_Cutting@fws.gov (K.A. Cutting).

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development, and urbanization (Knick et al., 2003). Across the biome, strong environmental gradients exist, driven largely by elevational-mediated soil temperature and moisture levels that are expressed by spatial changes in a multitude of sagebrush species and subspecies (hereafter: *sagebrush type*). Current conservation has largely ignored the effect of sagebrush type, largely due to methodological limitations of identifying sagebrush type at large scales. In the northern Rocky Mountains, distinct zonations of sagebrush type exist. Given these differences, predator activity, abiotic and biotic characteristics, and grazing might ultimately influence the animal communities differently across these sagebrush types. Understanding the contribution of different sagebrush types to components of fitness in animals can help prioritize conservation to those sagebrush types that contribute most to their population growth.

The greater sage-grouse (*Centrocercus urophasianus*; hereafter: *sage-grouse*) is an umbrella species that needs large tracts of habitat which is also dependent upon by many other species found in the sagebrush biome of the American West (Rowland et al., 2006). Sage-grouse have declined across their range from millions to now only 200,000 individuals, and their current range is half of the historic extent (Schroeder et al., 2004). Sage-grouse reproductive success is highly dependent on the structure and function of sagebrush habitats including relationships with shrub, grass, and forb thresholds (Connelly et al., 2000). Non-persistent stressors affecting sage-grouse populations include anthropogenic structures (Hovick et al., 2014).

Cattle grazing is the most common land-use practice in the American West (Knick et al., 2003). Grazing systems rely on intricate networks of linear and point features (hereafter: *LPF*; e.g. fences, water tanks), which have been shown to influence predator and prey populations (Dickie et al., 2017). Avian predators are more common in areas with increased LPFs (e.g., water tanks; Coates et al., 2016), and mortality from collisions with LPFs (e.g. fencelines) occurs frequently (Stevens et al., 2013; Van Lanen et al., 2017). Indirect effects of LPFs on animal behavior include avoidance and movement patterns through increased habitat edges, anthropogenic noises, and artificial light (Kociolek et al., 2011). Recent studies have revealed that LPFs also allow predators to travel farther over shorter times, which enhances their search efficiency and prey-handling time (Dickie et al., 2017; DeMars and Boutin, 2017). However, impacts of LPFs related to grazing systems on behavioral cues and survival outcomes remains unknown, and are currently a research priority (Hovick et al., 2014).

Using the sage-grouse as our model species, we examined data on nesting ecology in a grazing-dominated landscape located in the northern Rocky Mountain region to (1) identify how they select nest sites based on sagebrush types that might result in maladaptive selection and (2) to evaluate whether a variety of suspected characteristics related to grazing LPFs and other biotic and abiotic characteristics might influence possible mismatches between selection cues and survival outcomes. We hypothesized that adaptive selection would be strongly influenced by sagebrush type driven by large differences in hiding cover, microclimate and/or predator travel routes and perches. We further hypothesized that reduced nest survival outcomes would be associated with grazing infrastructure given suspected predator use of infrastructure features for travel corridors and/or perches that increase their search efficiency and kill rates.

2. Materials and methods

2.1. Study area

We conducted the study on a 65,000-ha mountainous landscape in southwest Montana, USA, with the Greater Yellowstone ecosystem to the east and High Divide ecosystem to the west (see Fig. 1). The region is considered biologically diverse and supports a multitude of sagebrush types along with several breeding leks for sage-grouse as well as other charismatic megafauna including grizzly bears (*Ursus arctos horribilis*) and wolves (*Canis lupus*). Dominant stands of sagebrush types include: mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*; hereafter: *MTSA*), basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*; hereafter: *BBSA*), three-tip sagebrush (*Artemisia tripartita*; hereafter: *TTSA*) and low sagebrush (*Artemisia arbuscula*). Basin big sagebrush occurs in valley bottoms with deep soils, TTSA occurs at mid-elevation slopes, while MTSA occurs at the highest elevations. Low sagebrush was excluded from further consideration because birds did not use this sagebrush type for nesting. The dominant land-use practice includes livestock grazing with virtually all of the landscape receiving recent grazing activity. In most years, cattle begin grazing in low and basin big sagebrush during late-May and progress to higher elevation stands of TTSA and MTSA following the advancement of vegetation phenology. Most of the study area is on a rest-rotation grazing system, where a particular pasture is grazed for two-to-three years followed by a year of rest. Average stocking rate varies 1.2–2.0 ha per adult cow (weighting 454 kg; Ryan Martin, *personal communication*). An intricate network of grazing related LPFs that supports this agro-pastoral landscape includes: fences, water tanks, paths, and roads.

2.2. Female capture, measurement, and marking

We captured adult female sage-grouse across ten breeding leks using spotlights and dip nets from 2014 to 2016 (2014: $n = 51$, 2015: $n = 55$, and 2016: $n = 57$). We marked each female with either a 22-g (Advanced Telemetry System, Isanti, MN) or 12-g transmitter (American Wildlife Enterprises, Monticello, FL) necklace-style transmitter. Both transmitter types are < 5% of the body weight; a threshold believed to have minimal impacts on flying animals (Cochran, 1980). This research was conducted in compliance with state (2014-050, 2015-23, 2016-049), and animal care/use (2012-40, 2015-30) permits.

2.3. Bird tracking and nest monitoring

We tracked prenesting females 2–3 times per week from mid-April until mid-July during the three years of study (see Fig. 1). After we discovered a nest, we monitored its survival 2 times per week until it successfully hatched ≥1 egg (as determined by the presence of a chick in the nest bowl, or evidence of an intact egg membrane that indicated hatching had occurred) or was destroyed by a predator. We assessed whether a nest was still active by using radio-telemetry from established points and bearings from an established location; usually 50–100 m away. We censored five nests from analysis of abandoned nests because the abandonments were believed to have been caused by observer disturbance. No failures were linked to cattle trampling. The community of nest predators includes coyotes (*Canis latrans*), ravens (*Corvus corax*), badgers (*Taxidea taxus jacksoni*), wolves and grizzly bears, with the first three species suspected of being responsible for most nest losses (*Kyle Cutting*, personal observation).

2.4. Sagebrush type

We visually mapped four sagebrush types across the study area through detailed field mapping surveys of continuous patches > 0.25 ha that were dominated (> 50% cover) by a given sagebrush type. We assessed the accuracy of these visual surveys to the manual surveys described below and found high assignment accuracy (95.6% accuracy).

2.5. Linear and point feature variables

We used Google Earth (image date: 19 July 2014) to quantify distances from nest and random points to the nearest path. We could not differentiate between paths of cattle and those of wild ungulates, but based on our experience in the study area we think most paths were predominantly created by cattle given evidence of their tracks and

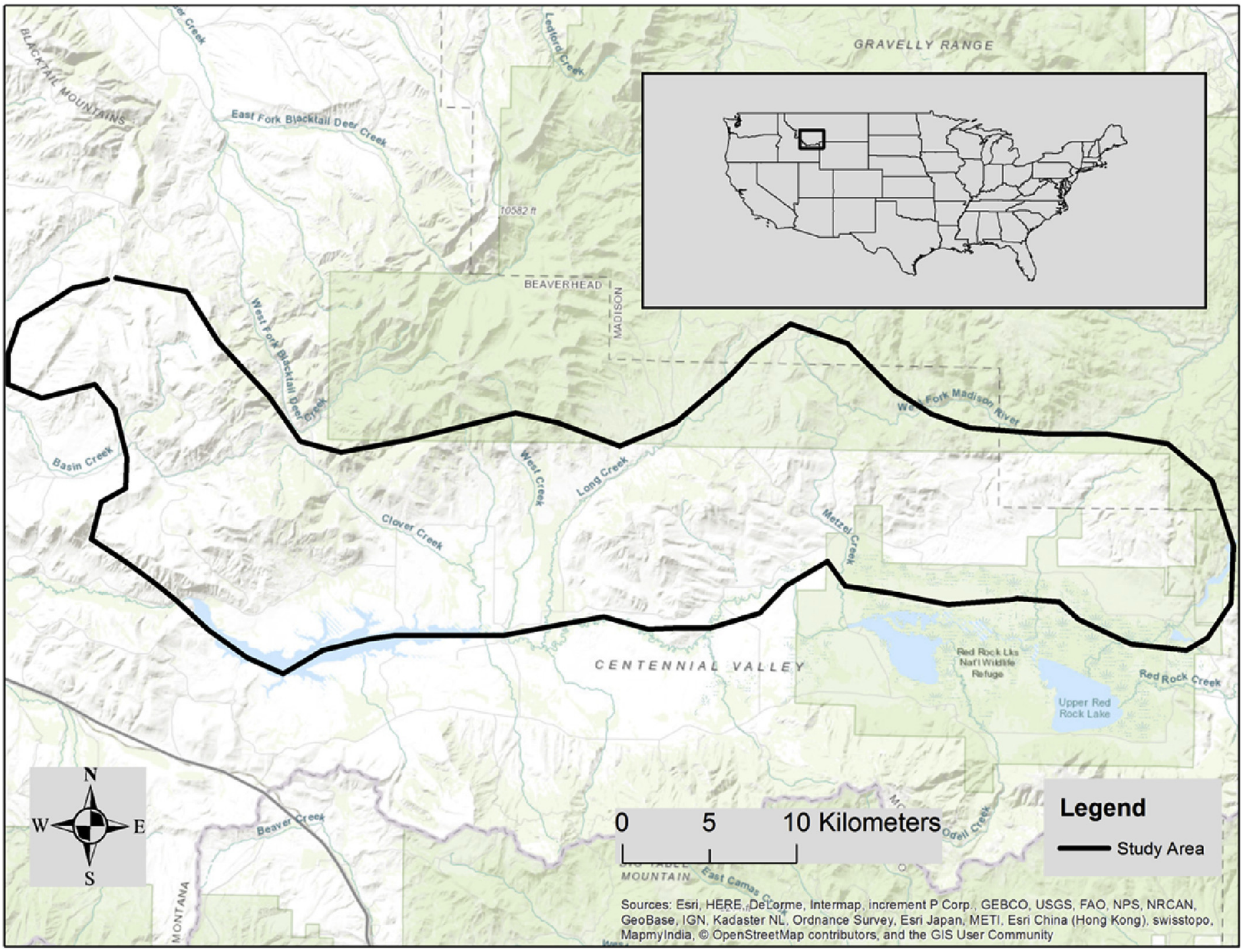

Fig. 1. Map of the study area location in southwest Montana, USA.

feces, as well as most paths led to water tanks, fences, and roads used by livestock producers. Wild ungulates (elk [*Cervus elaphus*] and mule deer [*Odocoileus hemionus*]) also help maintain the network of paths. We compiled information on water tanks, roads and fences using existing data from our partners on grazing infrastructure for the study area. Roads are also utilized by recreationalists pursuing hunting and motorized use and are generally considered to have minimal to light traffic throughout the year. We confirmed, and modified when necessary the relevant existing data layers based on results of intensive field surveys. We used ArcGIS10.5.1 (ESRI, Redlands, California, USA) to measure distances from nests and random points to LPFs.

2.6. Biotic variables

We measured vegetation characteristics (i.e. live grass, dead grass, forb, and shrub) at nests at fate (either successful or predated) and at random locations throughout the nesting season. To assess selection patterns for nest sites, we stratified the number of random survey points based on the availability of a particular sagebrush type as determined by our visual mapping surveys using GIS. We conducted vegetation surveys at an average of 2.4 random points to every nest; with the number of random points varying based on the availability of a given sagebrush type (MTSA = 3.1, TTSA = 2.1, and BBSA = 1.3). We collected biotic plant data at 1-m intervals along three 30-m transects equally spaced at 120° using a modified version of the line-point intercept method described by Herrick et al. (2017). We expected plant cover to vary according to sagebrush type with BBSA having the lowest, whereas MTSA having the highest. Therefore, we collected cover data on a vertical plane (height and number of times it crossed the plane) of up to four plant species at each sampling point, resulting in plant cover estimates exceeding 100%. We limited the number of species to four since this was generally the maximum number of different species that intersected the vertical plane across the various sagebrush types. If the number of layer 'hits' was still < 4, we then recorded the type of ground surface present (e.g. litter, bare ground, rock, moss). At each stop along the vegetation transects, we dropped a pin flag and measured the height and cover of multiple vegetation layers along this vertical plane. We recorded different plant species that touched this plane beginning at the highest layer and proceeding to the lowest layer. The only time we recorded the same species was when it occurred as both dead and alive. This approach allowed us to characterize plant coverage estimates that exceed $> 100\%$. Accumulated cover estimates best characterize the known differences in complexity of the plant community across the various sagebrush types; given the lower layers provide additional concealment from predators. We centered each transect either over a nest bowl, or for the case of transects associated with random points, a randomly chosen nesting shrub > 30 cm in height. Given the influence of vegetation cover on nest survival is dependent on the stage of the growing season, we controlled for the effect of growing season phenology on grass cover by following guidelines described in Gibson et al.

(2016). As a proxy for previous grazing intensity, we recorded density of cow defecation piles within 1-m of either side of each transect.

2.7. Abiotic variable

Terrain with a steep southwest facing aspect has the highest heat loading while terrain with steep northeast facing aspects has the lowest. Because snowpack is deeper and persists longer on north facing aspects, we predicted that heat loading would positively influence nest-site selection behavior given how early sage-grouse initiate nests in the spring, but would have marginal effects on nest survival (Gregg et al., 1994; Sveum et al., 1998; Doherty et al., 2014). We calculated heat loading using the Geomorphic and Gradients toolbox (Evans et al., 2014) in ArcGIS. Weather patterns varied across years of study during the month of March, which is when lekking and prenesting behavior begins. Conditions in March of 2015 were, when compared to other years of study, warmer (average temperature: 2014 = −2.9 °C, 2015 = 0.4 °C, and 2016 = −2.1 °C) and drier (average precipitation: 2014 = 59.2 mm, 2015 = 8.3 mm, and 2016 = 58.2 mm; PRISM Climate Group, 2018), and snowmelt occurred nearly 2 weeks earlier (2014 = 4 May 2015 = 22 March, and 2016 = 23 April; Lakeview Ridge - 44° 35′ 00″ N, 111° 49′ 00″ W, 2350 m a.s.l., https://wcc.sc.egov.usda.gov/nwcc/site?sitenum=568).

2.8. Statistical analyses

We conducted two separate analyses directed at assessing whether selection behavior was adaptive across three sagebrush types and by considering variables from biotic, abiotic, and grazing related model suites. Response variables for both nest-site selection (used vs. available sites) and nest survival (survived vs. predated) were binary and evaluated using appropriate methods for such response variables (see below) to evaluate competing models. To choose among competing models, we employed an automated model-selection procedure to evaluate the variables that most influence selection and survival within our study system from across suites.

2.8.1. Selection analysis

To assess selection for particular sagebrush types, we used the Manly resource selection ratio (selection ratio = used/availability) as a measure for preference/avoidance patterns at the population level. A selection ratio > 1 indicates preference of a certain sagebrush type relative to its availability on the landscape, and a ratio < 1 indicates avoidance. We used the *adehabitat* package to assess nest-site selection (Calenge, 2006) in the R programming language (R Core Development Team, 2018).

Before conducting our analyses, we evaluated pairwise correlations and variance inflation factors (VIF) to assess possible collinearity issues in our covariates but did not find evidence of high multicollinearity (Pearson's $r \le 0.7$, VIF < 4). We hypothesized that the presence of grazing-related LPFs, cattle paths and road that provided predator travel corridors, and grazing infrastructure that provided perches for avian predator might be expected to negatively affect nests that were closer to such features and that nests placed in more topographically variable settings might be more obscured from predators. We therefore log-transformed all LPF variables to account for potential threshold effects. We used an exponential logistic resource selection function (RSF) to compare variables at nest sites with those at available sites using 99 bootstrap iterations. The RSF approach utilizes a used-available framework from a weighted distribution to generate a maximum likelihood estimate of the probability of use for each variable. We used the R package *Resource Selection* (Lele et al., 2017) to assess nest-site selection of variables spanning the three model suites (Table 1). We tested the fit of selection models to the data by applying the Hosmer and Lemeshow goodness-of-fit test using the *Resource Selection* package in R.

2.8.2. Nest survival analysis

We evaluated competing models of daily nest survival rates (hereafter: *DSR*) that allowed DSR to be a function of various combinations of variables from the LPF, biotic, and abiotic suites using generalized linear models with binomial distributed errors and a logit link (Dinsmore et al., 2002). We calculated nest survival rate (hereafter: *NSR*) as the probability that a nest with given covariate conditions would survive 38 days from the start of egg-laying through incubation. We used the delta method to calculate standard errors (Powell, 2007) on estimated DSR and NSR. We also evaluated whether survival decreased across the nesting season, and whether possible temporal patterns in DSR across sagebrush types might have corresponded with differences in vegetation phenology and snowmelt between sagebrush types at low versus high elevations. We did so by using two models: the first contained an additive term between nest initiation date and sagebrush type, and the second contained an interaction term between the same variables. We used Program MARK (White and Burnham, 1999) through the *RMark* package (Laake, 2013) and its functions for estimating daily nest survival (Dinsmore et al., 2002).

We ran all possible additive combinations of covariates to describe selection and DSR using the *MuMIn* package (Bartoń, 2017) in R. We assessed relative model support in two ways: (1) we considered the variables included in the best-supported model, i.e. the model with the lowest AIC_c score (Burnham and Anderson, 2002) and evaluated the magnitude of each estimated coefficient and the extent to which each coefficients in the model overlapped zero, and (2) we implemented model averaging across all models that were within 4 AIC_c units of the top model and evaluated features of those coefficients as we did for the top model. Model averaging of uninformative variables across a set of models increases parameter uncertainty and is of questionable utility when variables across a set of models have low variation in the direction and effect size (Cade, 2015). We found high agreement in both direction and magnitude of effect sizes from the two interpretation techniques for both the selection and survival analyses. Thus, for our specific case reported on here, we avoid redundancy by basing our inferences on just those coefficients found in the top model. To assess if the covariates in the most supported nest survival model varied across sagebrush type, we conducted an exploratory analysis by testing interaction effects between sagebrush type and each continuous variable and found no support for interactive effects.

3. Results

From 2014 to 2016, we monitored a total of 38 nests in BBSA, 69 nests in MTSA, and 47 nests in TTSA (Table 1). To assess selection patterns for nest sites, we collected data from a total of 365 random points across the three sagebrush types (BBSA: $n = 51$, MTSA: $n = 214$, and TTSA: $n = 100$, Table S1). A total of 56 nests hatched at least one egg (Table S2). All nest failures in the analyses were caused by nest predation.

3.1. Nest site selection

Female birds strongly selected stands of BBSA (7.5% of the study area), avoided stands of MTSA (63.5% of the study area) and exhibited no selection for TTSA (25.3% of the study area; Manly resource selection (mean ± 95% CI): BBSA = 3.29 ± 0.90, MTSA = 0.71 ± 0.12, TTSA = 1.21 ± 0.29). We did not find any females nesting in low sagebrush, which represents 3.7% of the study area.

A total of 35 models describing selection patterns were well-supported by the data (see subset of models on Table 2A). We did not find evidence of lack of fit problems with our most general model ($P = 0.10$, Hosmer and Lemeshow goodness-of-fit test, Table 2A). Estimates from the top model suggest females selected nest sites with less alive grass ($\hat{\beta}$= -0.013, SE = 0.005) and forb cover ($\hat{\beta} = -0.013$, SE = 0.003),

Table 1
Covariates used in the nest site selection and survival analyses. Each variable is categorized according to our main hypotheses.

Category	Variable	Description	Type
Biotic	Grass Cover	Accumulated cover of grasses	3 × 30 m transect
Biotic	Dead Grass Height	Accumulated height of dead grass	3 × 30 m transect
Biotic	Forb Cover	Accumulated cover of forbs	3 × 30 m transect
Biotic	Shrub Cover	Accumulated percent cover of shrubs	3 × 30 m transect
Biotic	Year	Annual effects	Factor
Biotic	Sagebrush Type	Dominant shrub type	Factor
Abiotic	Heat Load[a]	Combines aspect and slope	GIS 30m^2
Linear and Point	Road	Log distance to road	GIS
Linear and Point	Path	Log distance to path	Google Earth
Linear and Point	Fence	Log distance to fence	GIS
Linear and Point	Water tank	Log distance to water tank	GIS
Linear and Point	Cow pie	Log cow pie density	3 × 30 m transect

[a] Heat Load (Evans et al., 2014).

greater amounts of dead grass height ($\hat{\beta} = 0.001$, SE = 0.0004), higher amounts of heat loading ($\hat{\beta} = 1.782$, SE = 0.862; Fig. 2), and greater selection in year 2016 ($\hat{\beta} = 0.570$, SE = 0.240). Selection of nest sites was related to grazing LPFs in two divergent ways: birds tended to avoid cattle paths ($\widehat{\beta} = 0.195$, SE = 0.058) but tended to select nest sites that were closer to roads than expected based on the nature of available sites ($\hat{\beta} = -0.199$, SE = 0.067; Fig. 2).

3.2. Nest survival

A total of 45 nest survival models were well-supported by the data (see subset of models on Table 2B). Based on the average of the annual estimates for each sagebrush type from the top model, 38-day NSR is estimated as 0.083 (SE = 0.041), 0.311 (SE = 0.063), and 0.169 (SE = 0.058) in BBSA, MTSA, and TTSA, respectively.

Daily survival rate was higher for nests farther from fences ($\hat{\beta} = 0.156$, SE = 0.069). For example, in 2014, in TTSA, DSR ± 1SE (NS ± 1SE) changed from 0.937 ± 0.022 (NS = 0.085 ± 0.077) to 0.974 ± 0.009 (NS = 0.365 ± 0.133), respectively, as covariate distance to fence went from its 2.5% quantile to its 97.5% quantile value in the observed dataset (Fig. 3A). In the top model, DSR was negatively associated with cow pie density ($\hat{\beta} = -0.198$, SE = 0.099; Fig. 3B). As cow pie density ranged from the 2.5% quantile to its 97.5% quantile value in the observed dataset, DSR changed from 0.972 ± 0.009 (NS = 0.342 ± 0.132) to 0.942 ± 0.019 (NS = 0.104 ± 0.082), respectively. Nests with greater amounts of dead grass had lower DSR than those with lower amounts of dead grass ($\hat{\beta} = -0.001$, SE = 0.0005; Fig. 3C). When ranged from 2.5% to 97.5% quantile in the observed dataset, influence of dead grass height on DSR decreased from 0.973 ± 0.008 (NS = 0.367 ± 0.118) to 0.935 ± 0.028 (NS = 0.079 ± 0.090), respectively. Daily survival rate was higher for nests with greater amounts of grass cover ($\hat{\beta} = 0.010$, SE = 0.004; Fig. 3D). For example, in 2014, in TTSA, DSR changed from 0.942 ± 0.019 (NS = 0.104 ± 0.083) to 0.982 ± 0.007 (NS = 0.495 ± 0.150), respectively, as covariate grass cover went from its 2.5% quantile to its 97.5% quantile value in the observed dataset (Fig. 3D).

We found a common pattern that shows DSR increasing with increasing initiation date; regardless of what sagebrush type the nest was located in. For nests initiated on the same date, DSR was predicted to be highest in stands of MTSA intermediate in TTSA, and lowest in BBSA.

4. Discussion

Adaptive selection, where fitness is higher in preferred habitats, has been widely documented in animals (Chalfoun and Schmidt, 2012; Clark and Shutler, 1999). However, in human-modified landscapes, habitat selection can be maladaptive due to anthropogenic changes on the landscape. In our grazing-modified system, we observed a decoupling between selection behavior for nest sites and subsequent survival outcomes. Sage-grouse preferred stands of BBSA for nesting, yet overall nest survival in BBSA was one-fourth the rate for birds nesting in MTSA. We also found little support for congruence between factors associated

Table 2
Candidate models, AIC$_c$, ΔAIC$_c$, Akaike weight (w_i), log-likelihood (*LL*) and number of parameters (*K*) for nest site selection (A) and survival (B) of female sage-grouse in southwest Montana, 2014–2016. All models within 2 AIC$_c$ units from the model with lowest AIC$_c$ value are shown.

Model	AIC$_c$	ΔAIC$_c$	AIC$_c$ weights	Model Likelihood	K
(A) Selection					
Year + forbs + grass cover + dead grass + road + path + heat load	1750.01	0.00	0.19	−866.51	8
Year + forbs + grass cover + dead grass + road + path + heat load + shrubs	1750.14	0.13	0.18	−865.45	9
Year + forbs + grass cover + dead grass + road + path + heat load + water tank	1750.91	0.90	0.12	−865.84	9
Year + forbs + grass cover + dead grass + road + path + heat load + shrubs + water tank	1751.06	1.04	0.11	−864.77	10
Year + forbs + grass cover + dead grass + road + path + shrubs	1751.38	1.37	0.09	−867.20	8
Year + forbs + grass cover + dead grass + road + path + heat load + cow pie	1751.45	1.43	0.09	−866.10	9
Year + forbs + grass cover + dead grass + road + path + heat load + shrubs + cow pie	1751.83	1.82	0.08	−865.15	10
Year + forbs + grass cover + dead grass + road + path + heat load + fence	1751.87	1.86	0.07	−866.32	9
Year + forbs + grass cover + dead grass + road + path	1751.96	1.95	0.07	−868.60	7
(B) Survival					
Sagebrush type + year + fence + grass cover + dead grass + cow pie	672.92	0.00	0.24	−327.42	9
Sagebrush type + year + fence + grass cover + dead grass + cow pie + heat load	673.64	0.72	0.17	−326.77	10
Sagebrush type + year + fence + grass cover + dead grass + cow pie + water tank	674.38	1.47	0.12	−327.15	10
Sagebrush type + year + fence + grass cover + dead grass + cow pie + shrub	674.52	1.61	0.11	−327.22	10
Sagebrush type + year + fence + grass cover + dead grass + cow pie + forb	674.78	1.86	0.10	−327.34	10
Sagebrush type + year + fence + grass cover + dead grass + cow pie + road	674.85	1.93	0.09	−327.38	10
Sagebrush type + year + fence + grass cover + dead grass + cow pie + path	674.88	1.96	0.09	−327.39	10
Sagebrush type + year + fence + grass cover + dead grass	674.90	1.99	0.09	−329.42	8

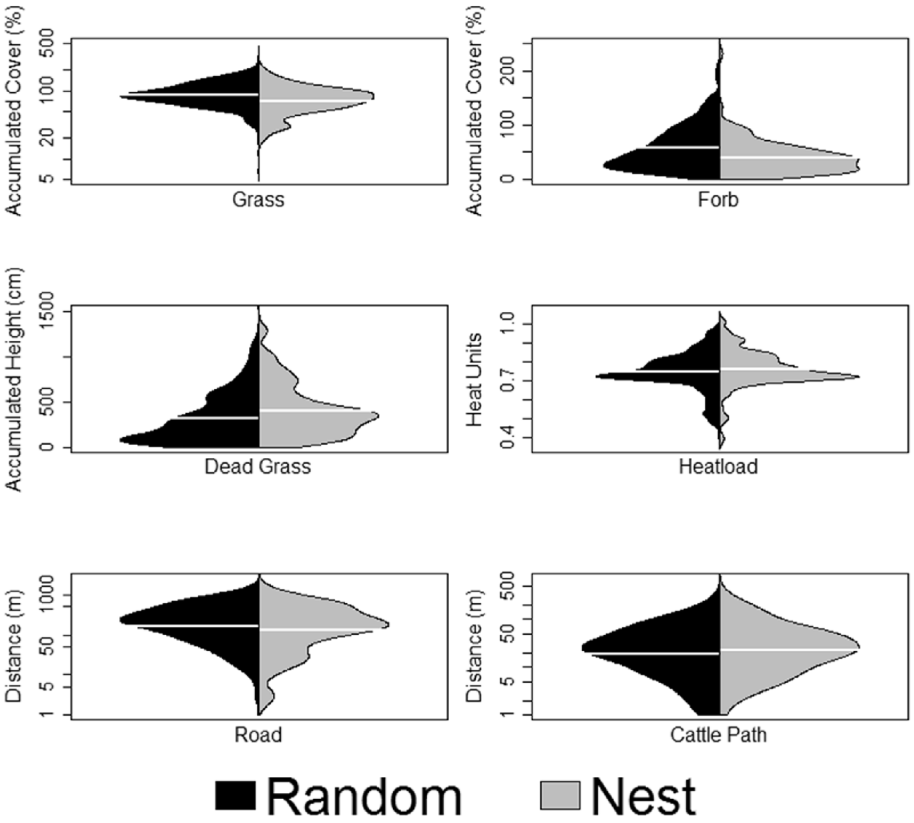

Fig. 2. Bean plots showing the distributions of parameters described in top model selection of nest sites and available sites. Shaded regions of the bean show density plots of the raw data. Mean values are indicated by white bolded lines.

with habitat selection and survival outcomes. Instead, we found support for indirect effects of grazing-related linear (fences) and point (cow pies) features that were associates with decreases nest survival in sage-grouse, a novel result for the species. Lastly, after controlling for grass phenology of live grasses, we found that live and dead grass had different relationships with nest survival. Collectively, these results have grazing implications, especially for public lands, where managers are trying to balance the need to provide high-quality wildlife habitat while simultaneously providing grazing opportunities to private livestock producers.

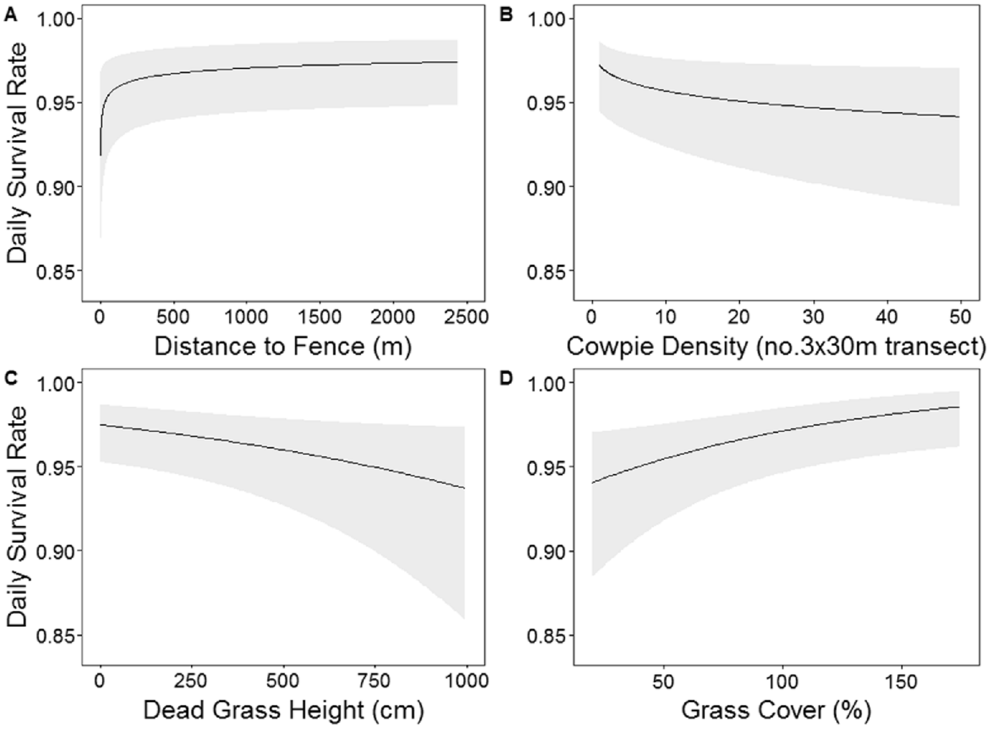

Fig. 3. Predicted daily survival rates for sage-grouse nests. Continuous covariates (distance to fence, cow pie density, dead grass height, and grass cover) were held at their mean values. Shaded region represents 95% confidence interval, whereas solid line shows mean effect. Relationship between daily survival rate and sagebrush type were similar for all continuous variables. The range of x-values goes from the 2.5%–97.5% quantiles of observed values in the data used in the analysis.

4.1. Factors influencing nest site selection

Our results indicate that sage-grouse prefer low-elevation sites for nesting. Such sites typically contain less snow and have advanced vegetation phenology relative to what is found in higher-elevation sagebrush types. Such differences are notable for sage-grouse on our study area because of how early in the year they start nesting relative to when snowmelt occurs. To our knowledge, this is the first study to document selection differences between sagebrush types. Our study site receives higher amounts of snowfall than other sagebrush regions in the American West. Thus, high-elevation sagebrush can hold snow later into the spring than sagebrush at lower elevations, resulting in delayed vegetation phenology. Females also tended to select nest sites in areas with greater amounts of heat, such as south facing aspects, which suggests that females might be attempting to reduce energy expenditure during times of low ambient temperatures. Interestingly, renesting rates were similar across elevations and birds did not switch sagebrush types between renesting attempts. These results collectively support our initial hypothesis that selection of nest sites would be favored in low rather than high elevations, and areas with greater amounts of heat.

The influence of herbaceous vegetation on sage-grouse nesting behavior and survival has received considerable attention, with most focusing on the height of dead grass (Connelly et al., 2004). In agreement with previous studies, we found that sage-grouse preferred nest sites with greater amounts of dead grass (Gregg et al., 1994; Sveum et al., 1998; Gibson et al., 2016). Grazing by domestic livestock during the growing season, in addition to compaction by deep snow during winter, can reduce the amount of standing vegetation the following spring, which leads to increased detection by predators. Although sage-grouse selected sites with higher amounts of dead grass for nesting, they also selected nest sites with lower grass cover from the current year's growth, supporting the hypothesis that females may be trying to balance tradeoffs between selecting sites that allow them to hide from predators while seeking sites that maximize localized movement and foraging efficiency for their precocial offspring (Gibson et al., 2017). Selection pressure was also greatest in 2016, a year with intermediate amounts of precipitation and temperature. Given temperature is expected to increase with climate warming, inter-annual variability in precipitation and other environmental factors may constrain to some degree the ability of sage-grouse to adapt to climate warming.

Sage-grouse avoid human structures (Hovick et al., 2014), yet no study has assessed LPF of grazing infrastructure on the birds' selection responses. Our selection analyses revealed that sage-grouse placed nests, on average, closer to roads and farther from cattle paths. Construction of primitive roads, which are largely found across our study site, oftentimes create edges that are angled towards the sun which increases the amount of heat at the ground surface during the nesting season. Given that cattle paths were the most ubiquitous LPF across the landscape, we suspect that predators might use cattle paths to navigate dense stands of sagebrush and thereby increase their kill rates and cause females to nest farther from paths. Dickie et al. (2017) found that wolves increased movement rates by selecting trails, and Atwood et al. (2004) reported that coyotes in rural landscapes selected linear habitat features. It would be useful if future research could assess path use by predators in sagebrush systems similar to ours.

4.2. Factors influencing nest survival

Our modeling results reveal differences in the contribution of sagebrush type to nest survival. Nests in BBSA had low survival rates (0.08 across our study), which was one-fourth the rate of nests in MTSA, and one of the lowest values ever reported for sage-grouse (Taylor et al., 2012). Growth form of BBSA is columnar (tree-like), with elongated trunks and branches well-above the ground surface, which increases sightability of ground-dwelling predators (Gregg et al., 1994). Basin big sagebrush also grows in valley bottoms where both snowmelt and onset of vegetative growth occur earlier in the spring compared to what is found in other sagebrush types (Barker and McKell, 1983), which likely causes predators to cue into these areas (Rose and Polis, 1998; Koehler and Hornocker, 1991). Nesting birds are forced to make the tradeoff between (a) nesting in snow-free areas with green vegetation but increased predation risk or (b) nesting in higher elevation areas that have delayed snowmelt and vegetation phenology but lower predation risk.

Nest survival across all the sagebrush types was lowest in 2015, a year when March temperatures were 2.5 °C warmer, and eight-times drier than in other years of our study. During 2015, the nesting season began 9 days earlier than in other years, which led to greater exposure of nests to predators because both nests and predators occur on a small portion of the overall landscape due to the distribution of snow, phenological stage of plants, and alternate foods, as demonstrated by the strong selection for low-elevation BBSA and avoidance of high-elevation MTSA. These results corroborate findings on sage-grouse from the Great Basin where reproductive success was reduced during years of warmer and drier conditions (Blomberg et al., 2013).

Assessments of indirect effects of LPFs related to grazing systems on both animal behavior and survival are rare (Hovick et al., 2014), even though they could be important for conservation planning if they exist. Indirect effects of LPFs on survival in animals might be even more severe than direct effects (e.g. fence collisions) because predators disproportionally use edge habitats, likely increasing interactions between predators and prey (Murcia, 1995). Even though fences did not influence selection patterns of female sage-grouse, we still found that females that nested closer to fences had lower rates of nest survival than those that nested farther away. Similarly, we also found that nest survival was negatively related to density of cow defecation piles near nest sites. Even though our study site historically evolved with grazing by wild bison, spatial patterns of bison are highly variable across years due to their nomadic behavior. In contrast, grazing by domestic livestock occurs more frequently and usually under more consistent stocking rates with more consistent timing, resulting in different forms of grazing pressure between wild versus domestic grazers. Given fences are utilized as a critical component of livestock grazing operations, modifications could occur to reduce perches for avian predators and to reduce edge effects that would increase predator movements through fences by increasing the height of the bottom strand of wire.

Live and dead grass amounts are of great interest to land managers given its importance to grazing management and wildlife conservation. Surprisingly, we found opposing effects of dead versus live grass on nest survival. Our results suggest a decrease in nest survival with increasing amounts of dead grass. After controlling for plant phenology, we found that grass cover from the current year's growth had a strong positive effect on nest survival. Variation in vegetation structure can greatly affect the distribution and detection probability of prey, which in turn can influence search and encounter efficiency by predators (Gorini et al., 2012). For instance, predators may be able to search most of the heterogeneous patches of dead grass within the sagebrush during the early season. In contrast, after the onset of the growing season when new grass is relatively more abundant, search and encounter efficiency by predators would be reduced. Future studies could assess the interactions between live versus dead grass on search efficiency and kill rates of predator communities across the growing season and sagebrush type.

5. Conclusions

We found that increasing live grass cover had the strongest, positive, association with nest survival as NSR varied by 39% across the range of grass cover measurements recorded. Other covariates had less but still measureable impacts on NSR which varied by 23–29% across the range of values recorded for variables including distance to fence, cow pie density, and dead grass, along with sagebrush type. It is important to note that the work reported here is focused only on the nesting aspect of the species' life history, when females appear to be making inappropriate decisions that could be leading to an ecological trap, especially in BBSA. Sage-grouse could compensate for the low observed nest survival in BBSA through increases in other vital rates such as chick survival. However, such compensation was not found in a previous study that found that chick survival was greater in high elevations (Gibson et al., 2017). Further, we found that adult survival during nesting was similar among sagebrush types, which suggests that females that nested in areas with lower nest survival rates were unable to compensate with increased adult survival. Basin big sagebrush could still be buffering against population stochasticity especially during winters of deep snowpack when other sagebrush types would be otherwise covered by snow forcing sage-grouse to migrate. Even though we did not find any birds nesting in low sagebrush, likely due to low stature and high amounts of bare ground, this sagebrush type is still important for lekking and for staging areas for bird's enroute to wintering quarters. Because agro-pastoral systems rely on grazing infrastructure to effectively implement targeted grazing practices, grazing systems that require the fewest amount of fences would be more desirable for use in sage-grouse nesting habitats. If this is not possible, we also speculate that (a) placing anti-perching devices on the top of fence posts and (b) increasing the height of the bottom strand of wire to reduce edge effects that are utilized by predators in search of nests in areas with fences. We are currently evaluating this idea by conducting an experiment in an area that supports high densities of nesting sage-grouse. Practitioners should seek to preserve and reduce threats in stands of MTSA, maintain cover of live grass in areas important for nesting, and modify fences to reduce search efficiency by predators.

Authors contributions

K.A.C., J.J.R., S.R.S., M.R.F., and B.F.S. conceived the idea, study design, and data collection. K.A.C., S.R.S., J.A.W., and E.N performed the field study. K.A.C. and J.J.R. with inputs from coauthors analyzed the data. K.A.C., J.J.R., and B.F.S. with critical inputs from all co-authors wrote the paper.

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Appendix A. Supplementary data

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References

Atwood, T.C., Weeks, H.P., Gehring, T.M., 2004. Spatial ecology of coyotes along a suburban-to-rural gradient. J. Wildl. Manag. 68, 1000–1009.

Barker, J.R., McKell, C.M., 1983. Habitat differences between basin and Wyoming big sagebrush in contiguous populations. J. Range Manag. 36, 450–454.

Bartoń, K., 2017. MuMIn: Multi-Model Inference, Version 1.40.0. https://cran.r-project.org/web/packages/MuMIn/index.html.

Blomberg, E.J., Sedinger, J.S., Nonne, D.V., Atamian, M.T., 2013. Seasonal reproductive costs contribute to reduced survival of female greater sage-grouse. J. Avian Biol. 44, 149–158.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach. Spinger, New York.

Cade, B.S., 2015. Model averaging and muddled multimodel inferences. Ecology 96, 2370–2382.

Calenge, C., 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Model. 197, 516–519.

Chalfoun, A.D., Schmidt, K.A., 2012. Adaptive breeding-habitat selection: is it for the birds? Auk 129, 589–599.

Clark, R.G., Shutler, D., 1999. Avian habitat selection: pattern from process in nest-site use by ducks? Ecology 80, 272–287.

Coates, P.S., Brussee, B.E., Howe, K.B., Gustafson, K.B., Casazza, M.L., Delehanty, D.J., 2016. Landscape characteristics and livestock presence influence common ravens: relevance to greater sage-grouse conservation. Ecosphere 7.

Cochran, W.W., 1980. Wildlife telemetry. In: Schemnitz, S.D. (Ed.), Wildlife Management Techniques Manual. The Wildlife Society, Washington, D.C, pp. 507–520.

Connelly, J.W., Schroeder, M.A., Sands, A.R., Braun, C.E., 2000. Guidelines to manage sage-grouse populations and their habitats. Wildl. Soc. Bull. 28, 967–985.

Connelly, J.W., Knick, S.T., Schroeder, M.A., Stiver, S.J., 2004. Conservation Assessment of Greater Sage-Grouse and Sagebrush Habitats: Report to the Western Association of Fish and Wildlife Agencies. WAFWA, pp. 610.

DeMars, C.A., Boutin, S., 2017. Nowhere to hide: effects of linear features on predator-prey dynamics in a large mammal system. J. Anim. Ecol. 87, 274–284.

Dickie, M., Serrouya, R., McNay, R.S., Boutin, S., 2017. Faster and farther: wolf movement on linear features and implications for hunting behaviour. J. Appl. Ecol. 54, 253–263.

Dinsmore, S.J., White, G.C., Knopf, F.L., 2002. Advanced techniques for modeling avian nest survival. Ecology 83, 3476–3488.

Doherty, K.E., Naugle, D.E., Tack, J.D., Walker, B.L., Graham, J.M., Beck, J.L., 2014. Linking conservation actions to demography: grass height explains variation in greater sage-grouse nest survival. Wildl. Biol. 20, 320–325.

Evans, J.S., Oakleaf, J., Cushman, S.A., Theobald, D., 2014. An ArcGIS Toolbox for Surface Gradient and Geomorphometric Modeling, Version 2.0-0. http://evansmurphy.wix.com/evansspatial Laramie, WY.

Gibson, D., Blomberg, E.J., Sedinger, J.S., 2016. Evaluating vegetation effects on animal demographics: the role of plant phenology and sampling bias. Ecol. Evol. 6, 3621–3631.

Gibson, D., Blomberg, E.J., Atamian, M.T., Sedinger, J.S., 2017. Weather, habitat composition, and female behavior interact to modify offspring survival in Greater Sage-Grouse. Ecol. Appl. 27, 168–181.

Gorini, L., Linnell, J.D., May, R., Panzacchi, M., Boitani, L., Odden, M., Nilsen, E., 2012. Habitat heterogeneity and mammalian predator–prey interactions. Mamm Rev. 42, 55–77.

Gregg, M.A., Crawford, J.A., Drut, M.S., DeLong, A.K., 1994. Vegetational cover and predation of sage grouse nests in Oregon. J. Wildl. Manag. 58, 162–166.

Herrick, J.E., Van Zee, J.W., McCord, S.E., Courtright, E.M., Karl, J.W., Burkett, L.M., 2017. Monitoring Manual for Grassland, Shrubland, and Savanna Ecosystems, Volume 1: Core Methods.

Hollander, F.A., Titeux, N., Holveck, M.J., Van Dyck, H., 2017. Timing of breeding in an ecologically trapped bird. Am. Nat. 189, 515–525.

Hovick, T.J., Elmore, R.D., Dahlgren, D.K., Fuhlendorf, S.D., Engle, D.M., 2014. Evidence of negative effects of anthropogenic structures on wildlife: a review of grouse survival and behaviour. J. Appl. Ecol. 51, 1680–1689.

Kociolek, A.V., Clevenger, A.P., St Clair, C.C., Proppe, D.S., 2011. Effects of road networks on bird populations. Con. Biol. 25, 241–249.

Koehler, G.M., Hornocker, M.G., 1991. Seasonal resource use among mountain lions, bobcats, and coyotes. J. Mammal. 72, 391–396.

Knick, S.T., Dobkin, D.S., Rotenberry, J.T., Schroeder, M.A., Vander Haegen, W.M., 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105, 611–634.

Laake, J.L., 2013. RMark: an R Interface for Analysis of Capture-Recapture Data with MARK. Alaska Fisheries Science Center Report 2013–01. NOAA, National Marine Fisheries Service, Seattle, Washington, USA.

Lele, S.R., Keim, J.L., Solymos, P., 2017. Package 'ResourceSelection.' R Package Version 0.3-2. https://cran.r-project.org/web/packages/ResourceSelection/ResourceSelection.pdf.

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. 28 (9), 552–560.

Noss, R.F., LaRoe, E.T., Scott, J.M., 1995. Endangered Ecosystems of the United States: a Preliminary Assessment of Loss and Degradation, vol. 28 US Department of the Interior, National Biological Service, Washington, DC, USA.

Powell, L.A., 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. Condor 109, 949–954.

PRISM Climate Group, 2018. Oregon State University. http://prism.oregonstate.edu created 26 Nov 2018.

R Core Development Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Robertson, B.A., Rehage, J.S., Sih, A., 2013. Ecological novelty and the emergence of evolutionary traps. Trends Ecol. Evol. 28, 552–560.

Robertson, B.A., Chalfoun, A.D., 2016. Evolutionary traps as keys to understanding behavioral maladapation. Curr. Opin. Behav. Sci. 12, 12–17.

Rose, M.D., Polis, G.A., 1998. The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. Ecology 79, 998–1007.

Rowland, M.M., Wisdom, M.J., Suring, L.H., Meinke, C.W., 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. Biol. Conserv. 129, 323–335.

Schroeder, M.A., Aldridge, C.L., Apa, A.D., Bohne, J.R., Braun, C.E., Bunnell, S.D., Kobriger, G.D., 2004. Distribution of sage-grouse in North America. Condor 106, 363–376.

Sveum, C.M., Edge, W.D., Crawford, J.A., 1998. Nesting habitat selection by sage grouse in south-central Washington. J. Range Manag. 80, 265–269.

Southwood, T.R., 1977. Habitat, the templet for ecological strategies? J. Anim. Ecol. 46, 337–365.

Stevens, B.S., Naugle, D.E., Dennis, B., Connelly, J.W., Griffiths, T., Reese, K.P., 2013. Mapping sage-grouse fence-collision risk: spatially explicit models for targeting conservation implementation. Wildl. Soc. Bull. 37, 409–415.

Taylor, R.L., Walker, B.L., Naugle, D.E., Mills, L.S., 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. J. Wildl. Manag. 76, 336—347.

Van Lanen, N.J., Green, A.W., Gorman, T.R., Quattrini, L.A., Pavlacky Jr., D.C., 2017. Evaluating efficacy of fence markers in reducing greater sage-grouse collisions with fencing. Biol. Con. 213, 70–83.

White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Hous. Theor. Soc. 46 (Suppl. l), 120–139.